

Paleovegetation reconstruction using $\delta^{13}\text{C}$ of Soil Organic Matter

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Abstract. The relative contributions of C_3 and C_4 plants to vegetation at a given locality may be estimated by means of $\delta^{13}\text{C}$ of soil organic matter. This approach holds a great potential for paleoecological reconstruction using paleosols. However, two main uncertainties exist, which limits the accuracy of this application. One is ^{13}C -enrichment as the plant carbon becomes incorporated into soil organic matter. The other is due to environmental influences on $\delta^{13}\text{C}$ of plants. Two types of data were collected and analyzed with an objective of narrowing the error of paleovegetation reconstruction. First, we investigated $\delta^{13}\text{C}$ variations of 557 C_3 and 136 C_4 plants along a precipitation gradient in North China. A strong negative correlation is found between the $\delta^{13}\text{C}$ value of C_3 plants averaged for each site and the annual precipitation with a coefficient of $-0.40\text{‰}/100\text{mm}$, while no significant coefficients were found for C_4 plants. Second, we measured $\delta^{13}\text{C}$ of soil organic matters for 14 soil profiles at three sites. The isotopic difference between vegetation and soil organic matter are evaluated to be 1.8‰ for the surface soil and 2.8‰ for the soil at the bottom of soil profiles. We conducted a sample reconstruction of paleovegetation at the central Chinese Loess Plateau during the Holocene and the Last Glacial (LG), and conclude that, without corrections for ^{13}C -enrichment by decomposition, the C_4 abundance would be overestimated. The importance and uncertainties of other corrections are also discussed.

1 Introduction

Carbon isotopic ratios of soil organic matter ($\delta^{13}\text{C}_{\text{SOM}}$) are close to those of the vegetation, and thus $\delta^{13}\text{C}_{\text{SOM}}$ can be used to estimate the relative abundance of C_3 and C_4 biomass

in the vegetation at a given locality in the past. Many researchers have used $\delta^{13}\text{C}_{\text{SOM}}$ of paleosols and/or loess to reconstruct paleovegetation and paleoclimate (e.g. Stanley et al., 1991; Boutton, 1996; Boutton et al., 1998; Guillaume et al., 2001; Wang and Zheng, 1989; Gu, 1991; Frakes and Sun, 1994; Han et al., 1996; Wang and Follmer, 1998; Lin et al., 1991; Ding and Yang, 2000; Vidic and Montañez, 2004; Liu et al., 2005; An et al., 2005). For reconstructions of paleovegetation, the following isotope mass-balance equations are used:

$$\text{C}_3(\%) = (\delta^{13}\text{C}_{\text{SOM}} - \delta^{13}\text{C}_{\text{C}_4}) / (\delta^{13}\text{C}_{\text{C}_3} - \delta^{13}\text{C}_{\text{C}_4}) \times 100; \quad (1)$$

$$\text{C}_4(\%) = 100 - \text{C}_3(\%) \quad (2)$$

where $\delta^{13}\text{C}_{\text{C}_3}$, $\delta^{13}\text{C}_{\text{C}_4}$ are the mean $\delta^{13}\text{C}$ values of C_3 and C_4 plants at a given locality at the time the soil under study was developed; $\text{C}_3(\%)$ and $\text{C}_4(\%)$ are percentages of C_3 and C_4 biomass in the local vegetation. The accuracy of the reconstruction depends upon the accuracy of the end member values of $\delta^{13}\text{C}_{\text{C}_3}$ and $\delta^{13}\text{C}_{\text{C}_4}$. The use of these equations also assumes that $\delta^{13}\text{C}_{\text{SOM}}$ represents the $\delta^{13}\text{C}$ value of bulk local vegetation.

To acquire the $\delta^{13}\text{C}$ values for the pure C_3 and C_4 plants at the time paleosols formed, isotopic values for modern plants are first obtained. However, modern plants may be isotopically different from ancient plants due to environmental changes. An array of environmental factors influence the $\delta^{13}\text{C}$ values of plants, and many scientists have investigated the effects (see the summary in Arens et al., 2000). Attempts have been made by several authors to correct the effects of these environmental factors before Eqs. 1 and 2 were applied (Liu et al., 2005; Chen et al., 2005).

Another source of uncertainty comes from the assumption that $\delta^{13}\text{C}_{\text{SOM}}$ equals the $\delta^{13}\text{C}$ of vegetation. It is known that ^{13}C -enrichment occurs during decomposition such that the soil organic matter tends to have higher $\delta^{13}\text{C}$ values than the vegetation (Troughton et al., 1974; Stout et al., 1975;



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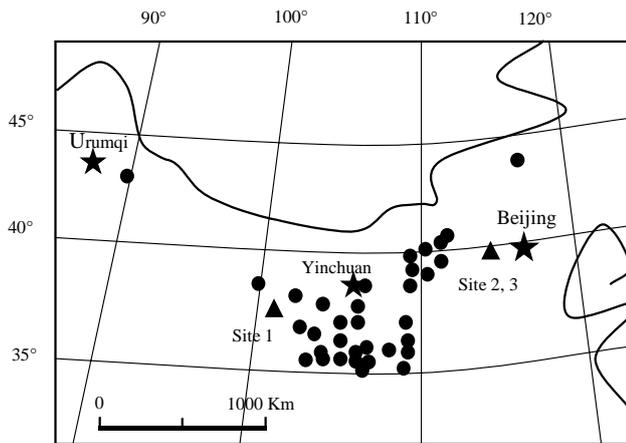


Fig. 1. Sample sites of this study. Solid circles and triangles represent plant and soil profile sites, respectively.

Schleser and Pohling, 1980; Balesdent et al., 1993; Boutton, 1996; Bird and Pousal, 1997). To our knowledge, this effect has not been taken into consideration when Eqs. (1) and (2) are used for paleovegetation reconstruction. It has been argued that using specific biomarkers, such as n-alkanes, this source of error can be ignored (Zhang et al., 2004). While this statement is likely but yet to be demonstrated, it is certain that ^{13}C -enrichment in the bulk soil organic matter relative to the vegetation due to decomposition should be corrected for.

This paper evaluates various corrections described above for paleovegetation reconstructions. We particularly focus on the precipitation effect on $\delta^{13}\text{C}$ in both C_3 and C_4 plants, and the ^{13}C -enrichment of soil organic matter relative to vegetation due to decomposition. We have collected new data for quantification these two effects.

New data are necessary because the existing data do not yield certain sensitivities for these two effects. Many studies have observed that $\delta^{13}\text{C}$ of C_3 plants decreases significantly with increases in precipitation (e.g. Ehleringer and Cooper, 1988; Smedly et al., 1991; Wang et al., 2003, 2005; Schulze et al., 2006). Liu et al. (2005) measured $\delta^{13}\text{C}$ of three C_3 species occurring in Northwest China, and found that the mean $\delta^{13}\text{C}$ decrease is 1.1‰ with every 100 mm increase in annual precipitation. This sensitivity is greater than that reported earlier by Steward et al. (1995) ($-0.34\text{‰}/100\text{ mm}$) and Wang et al. (2003) ($-0.49\text{‰}/100\text{ mm}$). Relative to C_3 plants, the $\delta^{13}\text{C}$ of C_4 plants is not sensitive to water availability (Farquhar et al., 1982; Henderson et al., 1992; Wang et al., 2005, 2006). Studies on C_4 species mostly showed slight increases in $\delta^{13}\text{C}$ with increasing water availability (Buchmann et al., 1996; Schulze et al., 1996; Wang et al., 2005, 2006). A counter example, however, is provided by Liu et al. (2005) who observed an opposite pattern in *Bothriochloa ischaemum* (C_4), i.e., $\delta^{13}\text{C}$ decreasing significantly with increasing precipitation ($-0.61\text{‰}/100\text{ mm}$). Our study includes an intensive investigation on the plants'

$\delta^{13}\text{C}$ response to precipitation in an arid and semiarid region by averaging a large number of species in 33 sites in North China with annual precipitation ranging from 15 to 650 mm.

The ^{13}C -enrichment in soil organic matter has been observed in both field and laboratory investigations. Some observations have come from field or laboratory incubation experiments (e.g. Natelhoffer and Fry, 1988; Wedin et al., 1995; Fernandez et al., 2003; Connin et al., 2001). Time spans used in these experiments are relatively short, typically less than 5 years, while the time for decomposition of organic matters in natural systems is much longer, on timescales from decades to millennia. Therefore, these short-term experimental results represented ^{13}C -enrichment only during the early stage of decomposition. In fact, progressive ^{13}C -enrichment continues even during decomposition of resistant soil organic matter having slow turnover rates (Chen et al., 2002; Feng et al., 1999; Torn et al., 2002). Other observations have come from isotopic measurements of soil profiles (e.g. Stout et al., 1978; Dzurec et al., 1985; Gregorich et al., 1995; Balesdent et al., 1993; Boutton, 1996; Bowman et al., 2002). Most of such studies aimed at understanding of vegetation dynamics, and thus study sites were chosen in areas where C_3/C_4 ratios of the local vegetation have not been constant in the past (e.g. Dzurec et al., 1985; Schwartz et al., 1986; Boutton et al., 1998; Guillaume et al., 2001; Krull et al., 2005). As a result, the observed $\delta^{13}\text{C}$ differences between soil organic matter and the standing vegetation included not only the ^{13}C -enrichment during organic matter decomposition, but also changes in the C_3/C_4 ratio of the local vegetation. To quantify ^{13}C -enrichment in soil organic matter, we studied isotopic variations in 14 soil profiles at three sites. All three sites are undisturbed, and have C_3 only vegetations; they are chosen especially because we intended to avoid isotopic variations in soil organic matter due to changing abundance of C_3 and C_4 plant types. We then evaluate how various corrections affect the paleovegetation reconstruction for the Chinese Loess Plateau.

2 Study sites and methods

2.1 Study sites of plant sampling and plant collection

A total of 33 sites in North China were studied, among which 27 sites are in Northwest China (Fig. 1 and Table 1). From west to east, North China is characterized by temperate arid, semiarid and semi-humid climate. The dominant control of the precipitation amount is the strength of the East Asian summer monsoon system. The precipitation occurs mostly in the summer season (from May to September), which accounts for approximately 68% to 87% of the total annual precipitation. From southeast to northwest in the study region, the annual rainfall amount decreases from 650 to 15 mm. The vegetation is dominated by shrubs and herbs. Plants were sampled in August of 1998 to 2005. In order to minimize

Table 1. The site-averaged $\delta^{13}\text{C}$ and number of plots and plant samples at each site as well as $\delta^{13}\text{C}$ of *Setaria viridis*.

Sites	Longitude (E'')	Latitude (N)	MAP (mm)	MAT ($^{\circ}\text{C}$)	N1	Site-averaged $\delta^{13}\text{C}$ (C_3)	S.D.	N2	Site-averaged $\delta^{13}\text{C}$ (C_4)	S.D.	N3	$\delta^{13}\text{C}$ of <i>Setaria viridis</i>
HL	109.25	35.6	631	9.4	0	-26.35	0.64	2	-12.5		1	-12.5
LC	109.4	35.7	621	9.2	7	-27.81	1.03	47	-12.57	0.68	24	-12.21
FXN	106.5	33.98	613	11.4	0	-27.1		1				
ZWL	108.7	36.1	600	9	0	-27.8		1				
XF	107.67	35.7	594	8.9	7	-27.7	1	70	-12.63	1.05	7	-12.5
CW	107.33	35.2	584	9.1	5	-27.38	0.9	30	-11.64	1.1	7	-10.8
FX	109.45	36	576.7	8.9	0				-13.73	0.68	4	
AS	109.33	36.75	531	8.8	5	-26.67	0.98	11	-12.35	1.14	4	-12
PL	106.67	35.55	511	8.6	3	-27.54	1.64	5	-12.05	0.07	2	-12
LX	103.2	35	501	6.3	4	-27.27	1.34	13	-12.46	0.87	5	-11.1
HQ	111.21	39.42	494	8.8	3	-27.8	1.26	6	-15.31	0.39	2	
DX	104.56	35.62	480	6.3	3	-27.55	2	6				
GY	106.27	36	478	6.2	2	-25.95	1.34	2	-11.8		1	
SM	110.27	38.81	440	8.5	2	-28.08	0.27	3	-13.8	1.05	4	-12.64
XJ	105.65	36	435	5.3	3	-26.44	0.6	5	-11.8		1	-11.8
ZGR	111.16	39.72	400	7.2	3	-26.72	1.11	6				
YZ	104.09	35.94	380	6.6	3	-26.2	1.75	8				
HZ	101.52	36.55	380	3	7	-26.61	1.29	45	-11.3		1	
DS1	110.8	39.81	380	5.6	3	-27.22	0.83	7	-12.6	0.34	2	
YL	109.65	38.5	365.6	8	2	-27.27	1.23	4				
DS2	109.95	39.75	360	5.5	4	-26.76	1.34	13	-12.33	0.28	4	
YJH	109.78	39.21	358	6.2	3	-27.33	1.04	10				
XLG	116.7	43.63	350	0.2	5	-26.42	1.03	43	-13.61	1.44	3	
LZ	103.83	36	327	6.6	4	-26.38	1.69	13	-12.7	0.61	3	
SN	99.63	38.81	280	3.6	4	-25.85	1.4	39	-12.95	0.35	2	-13.2
TX	105.8	37	277	8.4	1	-27.89	0.29	2	-13.22	0.95	3	-12.2
ZN	105.7	37.5	223	9.2	1	-26		1	-12.15	0.35	2	
YC	106.5	38.55	202	8.5	1	-26		1			1	-12.9
BY	104.1	36.55	194	8	14	-26.2	1.62	56	-12.64	1.02	21	-12.1
ZW	104.63	37.45	186	8.5	4	-25.78	2	80	-13.43	1.06	25	-11.77
JT	104.01	37.05	184	8.3	1	-23.5		1				
SD	101	38.16	180	5.7	1	-26.1	1.8	20	-13.2	1.97	2	
ALZ	105.6	38.5	150	7.8	1	-23		1				
TLF	89.5	42.9	15.6	13.94	1	-26.53	0.54	2	-14.23		1	

Abbreviation: MAP, mean annual precipitation; MAT, mean annual temperature; N1, number of plots; N2, number of C_3 plant samples; N3, number of C_4 plant samples; Site-averaged $\delta^{13}\text{C}$ data are weighted by C_3 and C_4 species biomass at a given site. HL, Huangling; LC, Luochuan; FXN, Fengxian; ZWL, Ziwuling; XF, Xifeng; CW, Changwu; FX, Fuxian; AS, Ansai; PL, Pingliang; LX, Linxia; HQ, Hequ; DX, Dingxi; GY, Guyuan; SM, Shenmu; ZGR, Zhongereqi; YZ, Yuzhong; HZ, Huangzhong; DS1, Dongsheng1; YL, Yulin; DS2, Dongsheng2; YJH, Yijingheluqi; XLG, Xilingereqi; LZ, Lanzhou; SN, Sunan; TX, Tongxin; ZN, Zhongning; YC, Yinchuan; BY, Baiyin; ZW, Zhongwei; JT, Jingtai; SD, Shandan; ALZ, Alashanzuoqi; TRF, Tulufan. In FXN (613 mm) and ZWL (600 mm) many C_3 species occur, but we did not collect plants by ourselves at the two sites, and the $\delta^{13}\text{C}$ data in this table were supplied by others who collected only one C_3 species at each site.

the influences attributed to human disturbance, local water supply, light regime and/or location within the canopy, sampling was restricted to unshaded sites far from human habitats. 107 plots with the size of $1 \times 1 \text{ m}^2$ or $2 \times 2 \text{ m}^2$ were laid out in these study sites (Table 1). How many plots that were set up in each study site depended on evenness of the plant distribution. The more even the distribution, the less the number of plots. For example, study sites in Shandan

(SD), Alashanzuoqi (ZQ), and Jingtai (JT) were situated in a desert, in which there are only 1–2 plant species and the plant distribution was very even. In this kind of area, one plot is sufficient. All above-ground biomass in each plot was harvested as completely as possible. Each plant species was weighed in the field, then was brought back to the laboratory for later measurement of the dry biomass. Plant samples brought back to the laboratory were oven-dried at 70° , then

weighed to get the dry biomass of each plant species. At each plot, 5–7 plants of each species were chosen, and the uppermost and the second fully opened leaves of each individual were obtained. The leaves from each species at each plot were mixed together into one sample for later $\delta^{13}\text{C}$ measurements. In total, 554 C_3 samples (including 255 species) and 132 C_4 samples (including 43 species) were collected.

2.2 Study sites of soil sampling and soil collection

One of the three soil sampling sites (Site 1) is located in the northeastern part of the Qinghai-Tibetan Plateau where the Chinese Academy of Sciences has a research station, the Haibei Highland Frigid Meadow Ecosystem Experimental Station (101°12' E, 37°45' N; 3200 m a.s.l.). The other two sites (Sites 2 and 3) are in the Donglingshan Mountain situated on the boundary between the Beijing and Hebei Provinces in North China, approximately 130 km west of Beijing city (Fig. 1). These two sites are within the Beijing Forest Ecosystem Research Station, which covers 16 000 ha of land, and was established on Donglingshan Mountain by the Chinese Academy of Sciences in 1990.

Site 1 has the characteristics of a highland continental climate, and is cold and humid with the mean annual temperature of -2.0°C and the mean annual precipitation of around 600 mm. Vegetation there is highland frigid meadow with most dominant species of *Potentilla fruticosa*, *Kobresia pygaea* and *Kobresia humilis*. There are no C_4 species. The soil type is alpine meadow soil. The area of Sites 2 and 3 is characterized by temperate semimoist climate. The amount of annual precipitation is 611.9 mm and the mean annual temperature is from 2°C (2303 m a.s.l. at the peak of Donglingshan Mountain) to 8°C (400 m a.s.l., Zaitang). The vegetation is characterized by forest, shrub and subalpine meadow. Site 2 is situated on the north-facing slope of Donglingshan Mountain at an elevation of 1600 m. The vegetation is a deciduous broad-leaved forest with only one birch tree species, *Betula platyphylla*, having an average height of 7 m and an average canopy area of 10 m^2 . In addition, two C_3 grass species, *Trullius chinensis* and *Galium verum*, about 0.15 m and 0.10 m high, respectively, are present within birch stands. No C_4 species is present at this site. The site has a brown forest soil. Site 3 is located on a ridge with an elevation of 1700 m, approximately 300 m southeast of Site 2. The vegetation at Site 3 is a subalpine meadow with *Roegneria kamoji* and *Artemisia lavandulaefolia* grasses as dominant species. Except for a few *Setaria viridis* (C_4) occurring on roadsides and near the climatic station, which is also located at the ridge (1700 m a.s.l.), no C_4 species exists elsewhere, particularly no C_4 species at the sampling plots. The soil type is subalpine meadow soil. There is no human settlement within 20 km^2 of Site 2 and Site 3, mainly because of strong winds and low temperature for many days of each year. Grazing and cutting have been strictly prohibited in the area since the 1980s.

At Site 1, six $0.5\text{ m}\times 0.5\text{ m}$ plots were laid out within one of the enclosures at the Haibei Highland Frigid Meadow Ecosystem Experimental Station with *Kobresia pygaea* and *Kobresia humilis* as dominant species. At each plot, all above-ground plants were collected (and will be used as litter input to the soil), and then the soil profile was dug to the weathered rock (saprolite). Soil profiles were sampled at 5 cm intervals. The depths of the six soil profiles are 60 cm, 120 cm, 110 cm, 60 cm, 70 cm and 90 cm, respectively.

At Site 2, five plots of $0.5\text{ m}\times 0.5\text{ m}$ were positioned in *Betula platyphylla* stands. In order to avoid birch roots, all plots were positioned 2–3 m away from tree trunks. At each plot, we first sampled the litter layer, and then dug a soil profile to the weathered rock. The depths of the five soil profiles are 75 cm, 105 cm, 100 cm, 100 cm and 120 cm, respectively. All soil profiles were sampled at 5 cm intervals except for one that was sampled at 10 cm intervals.

At Site 3, three plots of $0.5\text{ m}\times 0.5\text{ m}$ were sampled in the same way as described for Site 1. The depths of the soil profiles are 60 cm, 70 cm and 95 cm, respectively, and soils were sampled at 5 cm intervals.

2.3 Measurements

The plant and litter samples were oven-dried, and ground to pass a 0.3-mm mesh sieve. Soil samples were air-dried and sieved with a 2-mm sieve. Plant fragments and the soil fraction coarser than 2 mm were removed. The $<2\text{ mm}$ soil fraction was treated with 1M HCl at room temperature overnight to remove carbonates, after which it was washed and oven-dried at 70°C . Carbon contents and carbon isotopic ratios of samples were determined on an elemental analyzer coupled to a Delta Plus XP mass spectrometer in a continuous flow mode. The ^{13}C to ^{12}C ratio of the sample is reported in the δ -notation as the relative difference in parts per thousand (‰) from the V-PDB standard. The repeatability of C contents is better than 0.1% (1σ) and that of $\delta^{13}\text{C}$ is better than 0.15‰ (1σ).

3 Results

3.1 $\delta^{13}\text{C}$ variations of C_3 and C_4 plants with annual precipitation

The values of $\delta^{13}\text{C}$ in C_3 plants we measured range from -21.7‰ to -30‰ with a mean value of -26.7‰ ($n=557$, s.d.=1.56), and those of C_4 plants vary from -10.0‰ to -15.8‰ with a mean of -12.8‰ ($n=136$, s.d.=1.06).

Figure 2a plots the site-averaged $\delta^{13}\text{C}$ values of C_3 plants as a function of precipitation, showing that $\delta^{13}\text{C}$ increases significantly with decreasing precipitation with a slope of $-0.004\text{‰}/\text{mm}$ (s.e.= $0.001\text{‰}/\text{mm}$; one-tailed t -test, $P<0.001$). C_4 plant $\delta^{13}\text{C}$ values display a slightly increasing trend with increasing annual precipitation with

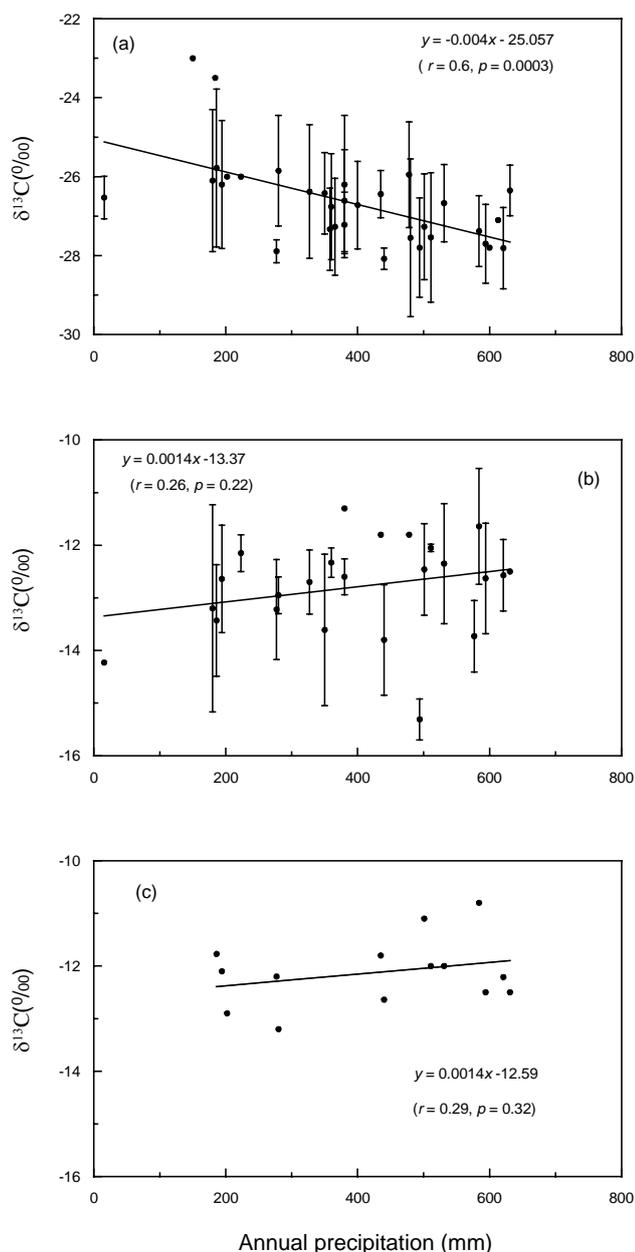


Fig. 2. Variations of site-averaged $\delta^{13}\text{C}$ in (a) C_3 plants, (b) C_4 plants, and (c) *Setaria viridis* (a C_4 species) with the annual precipitation amount along a rainfall gradient in North China. Each bar represents the site-averaged $\delta^{13}\text{C}$ value and the standard deviation of that site. Site-averaged $\delta^{13}\text{C}$ data are weighted by C_3 and C_4 species biomass at a given site. Points without error bars represent data from only one species (see Table 1).

a slope of $0.001\text{‰}/\text{mm}$ (s.e.= $0.001\text{‰}/\text{mm}$; two-tailed t -test, $P=0.220$), although the correlation is not significant (Fig. 2b). *Setaria viridis* (an annual grass with a stem length of 10–110 cm) is one of the most common C_4 species in China (Institute of Botany, CAS, 1987). Using this species alone, the $\delta^{13}\text{C}$ also slightly increases with precipitation,

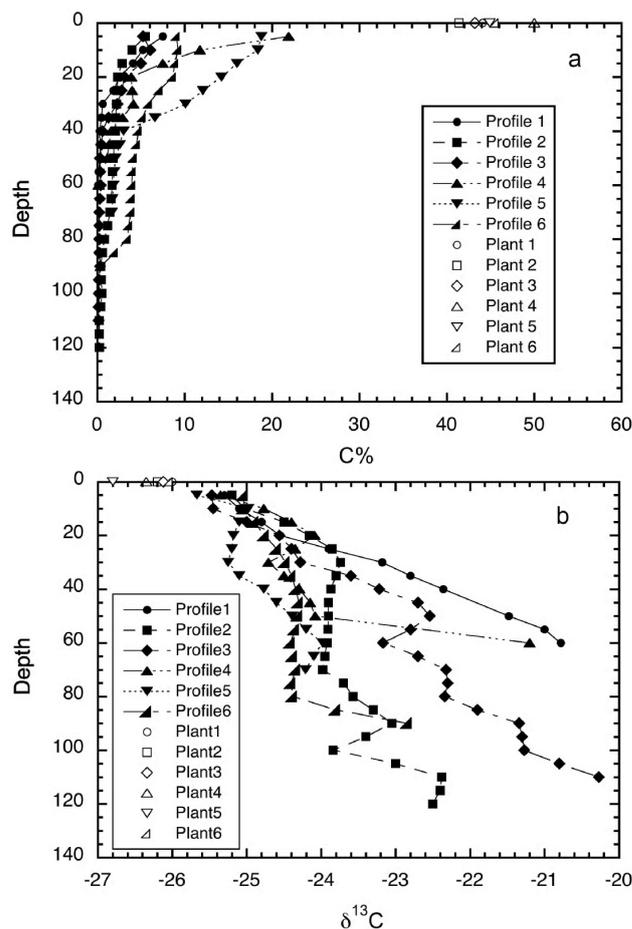


Fig. 3. Carbon contents (a) and $\delta^{13}\text{C}$ values (b) of soil organic matter and above-ground plants at Site 1.

with a slope of $0.001\text{‰}/\text{mm}$ (s.e.= $0.001\text{‰}/\text{mm}$; two-tailed t -test, $P=0.321$), but again the correlation is not significant (Fig. 2c).

3.2 Variations in $\delta^{13}\text{C}$ in soil profiles

In soils, the carbon content drops rapidly with depth near the surface, and then level off and slowly approaches zero in deeper layers. All three sites share this characteristic carbon distribution with depth. One example is given for Site 1 in Fig. 3a. The carbon isotopic ratio in the soil organic matter at Site 1 increases with depth (Fig. 3b). Compared to the carbon content (Fig. 3a), changes in $\delta^{13}\text{C}$ with depth are more gradual. The ^{13}C -enrichment with depth does not seem to approach a constant value within the depth of observation. Carbon isotope profiles at Site 2 and Site 3 (Fig. 4a and 4b) also show the typical pattern of ^{13}C -enrichment with depth.

We are mostly interested in the isotopic difference between vegetation and soil organic matter. Obviously, this difference depends upon which depth of soil is under discussion. When dealing with a paleosol, the specific paleo-soil

Table 2. Observed carbon isotopic differences between vegetation or plant litter and soil organic matter.

	Site 1		Site 2		Site 3	
	$\delta^{13}\text{C}_{\text{sur-veg}}$	$\delta^{13}\text{C}_{\text{botm-veg}}$	$\delta^{13}\text{C}_{\text{sur-litter}}$	$\delta^{13}\text{C}_{\text{botm-litter}}$	$\delta^{13}\text{C}_{\text{sur-veg}}$	$\delta^{13}\text{C}_{\text{botm-veg}}$
Profile 1	0.7	5.2	1.5	3.7	2.5	3.9
Profile 2	1.0	3.7	2.1	3.8	1.4	3.4
Profile 3	0.6	5.9	2.4	3.7	2.2	3.3
Profile 4	1.0	5.2	3.0	5.0		
Profile 5	1.1	2.6	2.5	4.5		
Profile 6	1.0	3.2				
Mean	0.9	4.3	2.3	4.1	2.0	3.5
Stand. error	0.1	0.5	0.2	0.2	0.3	0.2

The subscripts: sur=surface soil; botm=bottom soil; veg=vegetation; litter=plant litter at the soil surface.

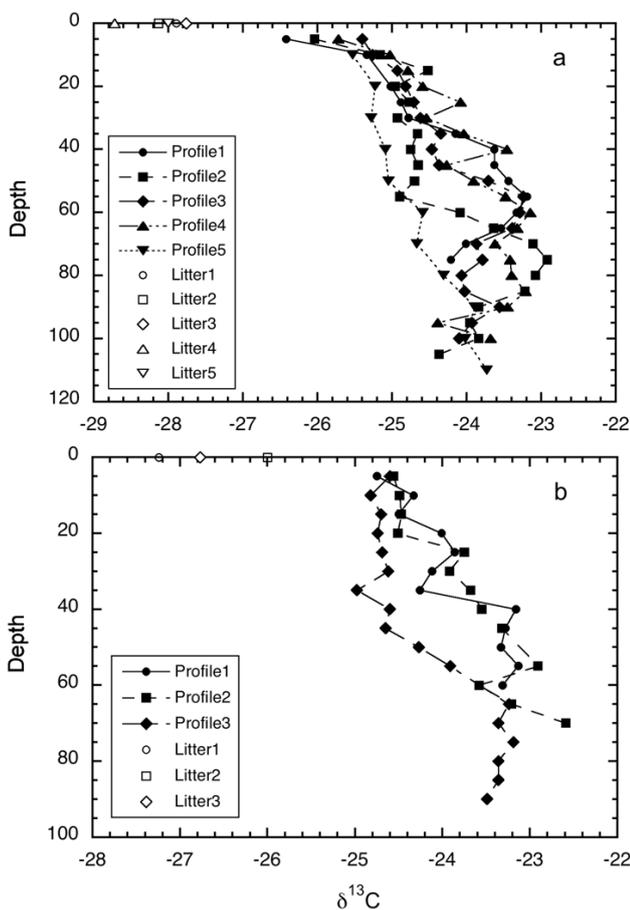


Fig. 4. Variations in $\delta^{13}\text{C}$ values of organic matter with depth at (a) Site 2, and (b) Site 3. The $\delta^{13}\text{C}$ value at the 0 cm depth of each profile is that of litter within each plot in (a), and above-ground plants in (b).

horizon it is not always clear. We therefore compiled in Table 2 observed $\delta^{13}\text{C}$ differences between vegetation (Sites 1 and 3) or litter (Site 2) and the soil organic matter either near the surface (0–5 cm of mineral soil) or at the bottom

of soil profiles. Between the surface soil and vegetation, the $\delta^{13}\text{C}$ difference ranges from 0.6 to 2.5‰ (Sites 1 and 3), and between the bottom soil and vegetation, the $\delta^{13}\text{C}$ difference ranges from 2.6 to 5.9‰. At the forested Site 2, the $\delta^{13}\text{C}$ difference is 1.5–3.0‰ between the surface soil and litter, and 3.7–5.0‰ between bottom soil and litter (Table 2). Typically, the $\delta^{13}\text{C}$ of litter on the forest floor is about 0.5‰ higher than the foliage input (e.g. Stout et al., 1978; Dzurec et al., 1985; Gregorich et al., 1995; Balesdent et al., 1993; Wang, 2003). If this enrichment is taken into account, the $\delta^{13}\text{C}$ difference between soil and vegetation would be 2.0–3.5‰ for the surface soil and 4.2–5.5‰ for the bottom soil.

4 Discussion

4.1 $\delta^{13}\text{C}$ variations of plants

For both C_3 and C_4 plants, water deficit usually causes plants to close stomatal pores to reduce water loss by transpiration, and thus the stomatal conductance (g) decreases. As a result, the ratio of intercellular to ambient CO_2 concentration (c_i/c_a) decreases. For C_3 plants, a decrease in c_i/c_a directly results in an increase in its carbon isotopic ratio (Farquhar et al., 1982). Observations of C_3 plant $\delta^{13}\text{C}$ values decreasing along a precipitation gradient reported by this work and others (e.g. Steward et al., 1995; Wang et al., 2005; Liu et al., 2005; Schulze et al., 2006) are consistent with the expectation. For C_4 plants, a decrease in the c_i/c_a ratio may lead to two opposite isotopic responses; the $\delta^{13}\text{C}$ may increase or decrease depending on the degree of leakiness, ϕ (Farquhar, 1983), the proportion of carbon dioxide produced within bundle sheath cells from C_4 acids that is not fixed by Rubisco but leaked back to mesophyll cells. According to the model developed by Farquhar (1983) (modified by Henderson et al., 1992), if the ϕ value is less than 0.35, the $\delta^{13}\text{C}$ of C_4 species decreases with decreasing c_i/c_a ratio; otherwise, $\delta^{13}\text{C}$ increases. The ϕ parameter seems to remain relatively constant for a given species under a wide

range of environmental conditions (e.g., temperature, moisture and light conditions). Henderson et al. (1992) found that the ϕ values measured in 10 C_4 species, using a gas exchange method, remained around 0.21 over a range of irradiance and leaf temperature. In this and other studies (Schulze et al., 1996; Buchmann et al., 1996; Ghannoum et al., 2002; Wang et al., 2005), $\delta^{13}\text{C}$ values of C_4 species were observed to decrease with increasing water stress, corresponding to ϕ values less than 0.35. Therefore, for the observation on *Bothriochloa ischaemum* by Liu et al. (2005) where the plant $\delta^{13}\text{C}$ significantly decreased with increasing annual precipitation amount, it is possible that the ϕ value of this species is greater than 0.35. *Bothriochloa ischaemum* seems to be a unique case, since it is the only C_4 species reported to have a negative $\delta^{13}\text{C}$ -precipitation correlation.

4.2 Variations in $\delta^{13}\text{C}$ and carbon content of soil organic matter

The soil profiles of carbon content and $\delta^{13}\text{C}$ show very different characteristics. The variation in carbon content with depth is very similar within all profiles at Sites 1 to 3 (Fig. 3a), which are similar to thousands of reported carbon distributions in soil profiles (Zinke et al., 1986, 1998). Typically, carbon content decreases rapidly near the surface, and then slowly in deeper soil. Judging from the carbon content profile alone it seems that limited soil processes are occurring at depth. Compared to the carbon content, the profile of soil $\delta^{13}\text{C}$ also shows relatively rapid change near the surface (although less so than that of carbon content), but the ^{13}C -enrichment continues in deeper layers. This suggests that even slow decomposition of resistant organic matter is associated with ^{13}C -enrichment.

Several mechanisms have been proposed to account for ^{13}C -enrichment of soil organic matter relative to original plants. The first mechanism is the decrease in the $\delta^{13}\text{C}$ of atmospheric CO_2 since the industrial revolution because of combustion of ^{13}C -depleted fossil fuels, and from the pre-industrial era to $\sim 11\,000$ ^{14}C yr BP, the $\delta^{13}\text{C}$ of atmospheric CO_2 was relatively constant, with a mean of -6.40‰ (Marino et al., 1992). This mechanism is responsible for an isotopic difference of about 1.3‰ between the pre-industrial organic carbon and the present vegetation (Marino et al., 1992; Leuenberger et al., 1992). The second mechanism involves different decay rates of various components in organic matter having different $\delta^{13}\text{C}$. These effects also significantly alter the total $\delta^{13}\text{C}$, but the expected magnitude and direction depends on the relative proportions of components, and are not completely known (Feng, 2002). The third mechanism is isotopic fractionation during decomposition. The most important processes are microbial respiration and fermentation, leading to ^{13}C -enrichment in microbial products compared to the organic substrate (Macko and Estep, 1984; Poage and Feng, 2004). This mechanism is considered to be the main

reason for observed ^{13}C -enrichment between litter and vegetation and with increasing soil depth.

The soil organic matter at the greatest depth of our soil profiles is likely derived from plant materials not affected by fossil fuel combustion, because soil organic matter in deep soils can be thousands of years old (Shen, 2000). We, therefore, subtract 1.3‰ from the observed mean $\delta^{13}\text{C}$ difference between deep soil and vegetation to account for the effect of the $\delta^{13}\text{C}$ decrease in atmospheric CO_2 since the industrial revolution. The $\delta^{13}\text{C}$ values of soil organic matter at 5 cm depth, may also have been affected by the $\delta^{13}\text{C}$ decrease in atmospheric CO_2 in recent decades. However, we did not measure the age of the soil organic matter, and thus cannot determine how much correction would be needed for the surface soil. We will use the observed difference without a correction for later discussions, but note here that this difference may be overestimated. The actual difference between vegetation and the surface soil would be between 0.5 and 1.8‰ (see discussion below). Summarizing the above discussions, we report that the mean $\delta^{13}\text{C}$ difference is 1.8‰ ($n=14$) between the surface soil and vegetation, and 3.0‰ ($n=14$) between the bottom soil and vegetation. If all estimates of isotopic differences between soil and vegetation are pooled, the difference is normally distributed with a mean of 2.3‰ and standard deviation of 1.1‰ ($n=28$).

Previous investigations (e.g. Stout et al., 1978; Dzurec et al., 1985; Gregorich et al., 1995; Balesdent et al., 1993) showed that the $\delta^{13}\text{C}$ difference between vegetation and the surface soil (down to 20 cm depth) varied between 0.5‰ and 2.5‰ . Wang (2001) obtained similar results from 36 soil profiles in Northwest China, and the mean $\delta^{13}\text{C}$ difference between vegetation and the surface soil layer (down to 15 cm depth) is 2.2‰ . These $\delta^{13}\text{C}$ differences obtained by previous studies were not corrected for the effect of the $\delta^{13}\text{C}$ decrease in atmospheric CO_2 .

The 3.0‰ carbon isotopic difference we obtained between the vegetation and the bottom organic matter is probably the maximum ^{13}C -enrichment due to organic matter decomposition, even though the fossil fuel effect has been corrected for, because most paleosols may not represent the soil at deepest horizons. If the $\delta^{13}\text{C}$ difference of 1.8‰ between the surface soil and vegetation is considered to be the most likely value for isotopic correction due to organic matter decay, Eq. (1) should be modified to be the following:

$$C_3(\%) = [(\delta^{13}\text{C}_{\text{SOM}} - 1.8 - \delta^{13}\text{C}_{\text{C}_4}) / (\delta^{13}\text{C}_{\text{C}_3} - \delta^{13}\text{C}_{\text{C}_4})] \times 100 \quad (3)$$

4.3 Reconstructions of paleovegetation

Equations (1) and (3) are mass balance equations for estimating the abundance of C_3 plants in the vegetation using the measured $\delta^{13}\text{C}$ of paleosol organic matter without or with a correction for ^{13}C -enrichment due to soil organic matter decomposition. Before using these equations, however, we

Table 3. Comparison of $\text{C}_4\%$ contribution to Paleovegetation with various corrections.

Holocene		$\delta^{13}\text{C}_{\text{C}_3}$	$\delta^{13}\text{C}_{\text{C}_4}$	Using Eq. 1*	Using Eq. 3*
				$\text{C}_4\%$	$\text{C}_4\%$
Today's vegetation		-27.5	-12.5	53.3	41
$\delta^{13}\text{C}_{\text{atm}}$ correction (+1.3‰)		-26.2	-11.2	44.7	32.7
CO_2 concentration correction (C_3 : +1.6)		-24.6	-11.2	38.1	24.6
Last glaciation		$\delta^{13}\text{C}_{\text{C}_3}$	$\delta^{13}\text{C}_{\text{C}_3}$	Using Eq. 1*	Using Eq. 3*
				$\text{C}_4\%$	$\text{C}_4\%$
Today's vegetation		-27.5	-12.5	34	22
$\delta^{13}\text{C}_{\text{atm}}$ correction (+1.3‰-0.3‰)		-26.5	-11.5	27.3	15.3
Precipitation correction (C_3 : +0.8‰)		-25.7	-11.5	23.2	10.6
CO_2 concentration correction (C_3 : +1.6‰+1.6‰)		-22.5	-11.5	0.9	-15.5

* Calculations assume that $\delta^{13}\text{C}_{\text{SOM}}$ is -19.5‰ for Holocene and -22.4‰ for LG.

also need to obtain the end member $\delta^{13}\text{C}$ values of C_3 and C_4 plants at the time when the plants grew. If we start with modern isotopic compositions of C_3 and C_4 plants, we have to make several corrections to obtain the $\delta^{13}\text{C}_{\text{C}_4}$ and $\delta^{13}\text{C}_{\text{C}_3}$ values for the time investigated in the geological history, e.g., Holocene or LG. These corrections account for the effects on plant $\delta^{13}\text{C}$ of (1) changes in precipitation, (2) changes in the $\delta^{13}\text{C}$ of atmospheric CO_2 , and (3) changes in the CO_2 concentration in the atmosphere. Here we use published loess $\delta^{13}\text{C}$ data for the Holocene and the LG in the Chinese Loess Plateau reported by Vidic and Montañez (2004) to show how different types of corrections affect the qualitative reconstruction of paleovegetation. We assume that all effects are linearly additive and there are no cross effects from more than one variable.

First, we obtain plant $\delta^{13}\text{C}$ values for the Holocene. The study site of Vidic and Montañez (2004) is located at Jiadao on the central Chinese Loess Plateau, which presently has a temperate semimoist climate with an annual precipitation amount of 577 mm. Our study shows that the mean $\delta^{13}\text{C}$ values of standing C_3 and C_4 plants in this area are -27.5‰ and -12.5‰ , respectively. For the Holocene, we could assume that precipitation was similar to the current level, and there is therefore no need to correct for the climate effect on plant $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ value of atmospheric CO_2 during the pre-industrial part of Holocene was 1.3‰ higher than it is today (Marino et al., 1992; Leuenberger et al., 1992). Thus, $\delta^{13}\text{C}$ values of C_3 and C_4 plants during Holocene would be -26.2‰ and -11.2‰ , respectively (Table 3).

Without the anthropogenic input of fossil fuel CO_2 , the atmospheric CO_2 concentration before the industrial revolution was 80 ppm lower than it is today. It is possible that the CO_2 concentration level also affects the $\delta^{13}\text{C}$ values of C_3 plants. However, the magnitude of this effect is not entirely clear. Polley et al. (1993) showed that C_3 plants, growing over a range of CO_2 concentrations characteristic of the Last

Glacial Maximum to the present atmosphere, tended to have constant c_i/c_a ratios, suggesting a constant carbon isotope discrimination (Δ). Feng and Epstein (1995), on the other hand, reported that the mean Δ value of tree rings in four trees is positively correlated to the CO_2 concentration with a mean slope of $0.02\text{‰}/\text{ppm}$. We have recently conducted a detailed study on the Δ response of ~ 50 tree-ring series from widely distributed locations to atmospheric CO_2 concentration changes during the past 100–200 years. We found that the pattern of the $\delta^{13}\text{C}$ response to CO_2 concentration changes is complex. Before 1950, the mean Δ value tended to increase with the CO_2 concentration increase, while since 1950 Δ has decreased. The instantaneous rate of Δ change with the CO_2 concentration varied systematically, ranging from $0.025\text{‰}/\text{ppm}$ in 1850 to $-0.013\text{‰}/\text{ppm}$ in 1995 (Wang and Feng, unpublished data). Apparently, the $\delta^{13}\text{C}$ response to changing CO_2 concentration was not linear during the past 100 years, and it is likely that this response not only depends upon the absolute level of CO_2 but also upon the rate of CO_2 concentration change. Thus, it is difficult to determine whether corrections for a CO_2 concentration change is necessary, and if so, how much correction should be made. Here we will make a paleoecological reconstruction considering the two situations, with and without a CO_2 concentration correction. Under the situation with the correction, we use the coefficient of $\delta^{13}\text{C}$ - CO_2 concentration of Feng and Epstein (1995) ($-0.02\text{‰}/\text{ppm}$), which has already been used by several previous authors. The average $\delta^{13}\text{C}$ value of C_3 plants would then be -24.6‰ in the Holocene after a 1.6‰ correction for an 80 ppm change in the CO_2 concentration of the atmosphere. For C_4 plants, $\delta^{13}\text{C}$ is not sensitive to CO_2 concentration change (Henderson et al., 1992), so it remains -11.2‰ (Table 3).

We now obtain $\delta^{13}\text{C}_{\text{C}_4}$ and $\delta^{13}\text{C}_{\text{C}_3}$ values for the LG. Atmospheric CO_2 concentration which was 80 ppm lower, and $\delta^{13}\text{C}$ value of CO_2 which was 0.3‰ lower than that of the

Holocene (Marino et al., 1992; Leuenberger et al., 1992). With no correction for the effect of CO_2 concentration, the $\delta^{13}\text{C}$ values of C_3 and C_4 plants in the LG become -26.5% and -11.5% , respectively. With corrections for the effect of CO_2 concentration, $\delta^{13}\text{C}$ values of C_3 plants in the LG become -23.3% . The $\delta^{13}\text{C}$ value of C_4 plants is still -11.5% .

In addition, the precipitation at the study site during the LG was about 200 mm lower than that in the Holocene (Wu et al., 1995). Assuming that the temporal sensitivity of ecosystem $\delta^{13}\text{C}$ in response to precipitation is the same as the spatial sensitivity we determined for the modern environment, we correct for the precipitation effect on the $\delta^{13}\text{C}$ of C_3 plants using the $\delta^{13}\text{C}$ -precipitation coefficient of $-0.4\%/100$ mm obtained in this study, which yields a 0.8% correction for C_3 plants. Therefore, the $\delta^{13}\text{C}_{\text{C}_3}$ of vegetation becomes -25.7% without the correction for the CO_2 concentration, and -22.5% with the CO_2 correction. The precipitation change does not significantly affect the $\delta^{13}\text{C}_{\text{C}_4}$ value, and thus no further corrections are made for the $\delta^{13}\text{C}$ of C_4 plants. Values for various corrections are listed in Table 3.

The average $\delta^{13}\text{C}_{\text{SOM}}$ value of S_0 (Holocene paleosol) is reported to be -19.5% , and that of L_1 (loess from the LG period) -22.4% (Vidic and Montañez, 2004). Table 3 shows the effect of each type of correction on the estimate of C_4 plant abundance in the vegetation of a given age. One important comparison is shown by the difference using Eq. 1 versus Eq. 3 (columns 4 and 5, respectively). Other things being equal, a correction for ^{13}C -enrichment due to organic matter decomposition yields a C_4 plant abundance in the vegetation about 12% lower than that obtained without such a correction.

The correction for CO_2 concentration causes an additional decrease in the estimated C_4 plant abundances. In the Holocene, the CO_2 concentration correction reduces the estimated C_4 abundances by about 6–8%. The effect is more substantial for the LG; the estimated C_4 abundances become 0.9% using Eq. (1) but negative using Eq. (3). The negative value indicates that we may have overcorrected either for the enrichment of soil organic matter, or the $\delta^{13}\text{C}$ end member of C_3 plants, or both. As discussed earlier, our recent compilation on tree-ring $\delta^{13}\text{C}$ series does not yield a mean sensitivity of $-0.02\%/ppm$. The highest sensitivity, $-0.013\%/ppm$, was obtained for the most recent year in the series (1995), and before 1995 it was consistently lower. Overcorrection for the effect of decomposition is also possible and is discussed below. Nevertheless, our calculations suggest that the C_4 abundance was probably very low during the LG. During the LG, the mean annual temperature was expected to have dropped by 8–10°C compared to the Holocene in the Chinese Loess Plateau (Wu et al., 1995; Ganopolski et al., 1998). The annual temperature today in Jiaodao is around 8.9°C. If the annual temperature for the Holocene is close to this value, the annual temperature during the LG time might have approached 0°C, close to the mean annual

temperature at the peak of Donglingshan Mountain in North China (2303 m a.s.l.; Site 2 and 3 are in Donglingshan Mt., Fig. 1), where no C_4 species are present above 1750 m (Liu, 2003). In addition, an investigation in Northwest China (including the Loess Plateau) showed that C_4 species in natural vegetation are rarely found at sites with annual temperatures below 3°C (Wang, 2001). Thus, it is likely that our estimated low abundance of C_4 plants during the LG is realistic.

Compared to previously published paleovegetation reconstructions the estimated C_4 abundances from this study are lower. Vidic and Montañez (2004) reported 53% for $\text{C}_4\%$ in the Holocene, and 34% in the LG. Liu et al. (2005) also reported 53% of C_4 vegetation in the Holocene, but 11% in the LG.

The differences in the percentage of C_4 plants between this study and those by Vidic and Montañez (2004) and Liu et al. (2005) derive from two sources. First, neither Vidic and Montañez (2004) nor Liu et al. (2005) considered the ^{13}C -enrichment during decomposition of organic matter (1.8‰ used in this study). Second, their corrections to obtain end members of $\delta^{13}\text{C}_{\text{C}_3}$ and $\delta^{13}\text{C}_{\text{C}_4}$ differ from ours. Vidic and Montañez (2004) did not make any correction, and therefore they obtained 53% and 34% C_4 contribution in the Holocene and the LG, respectively (see Table 3). When estimating the $\text{C}_4\%$ for the LG, Liu et al. (2005), made corrections for the precipitation effect on plant $\delta^{13}\text{C}$ of both C_3 and C_4 plants ($-1.1\%/100$ mm, $-0.61\%/100$ mm for C_3 and C_4 plants, respectively). Liu et al. (2005) also corrected for the effect of CO_2 concentration ($-0.02\%/ppm$), but they did not consider the fact that the $\delta^{13}\text{C}$ value of CO_2 was 1.3‰ higher during pre-industrial times Holocene than it is today.

4.4 Uncertainties

Uncertainties in paleovegetation reconstructions may originate from several sources. Of all the corrections considered, the most robust is the one related to changes in $\delta^{13}\text{C}$ of the atmospheric CO_2 . These changes are well known from the ice core data, and the physical mechanism is sound. However, this does not exclude the possibility that plants or the organic matter in a paleosol do not record the $\delta^{13}\text{C}$ value of CO_2 in the open atmosphere. If CO_2 recycled from organic matter decomposition or plant respiration is used in photosynthesis, a systemic error may be introduced. However, we consider this effect to be minor for grasslands, but should be considered when forest soils are investigated.

Correction for climate change, i.e., precipitation, in our study is exclusively based on modern vegetation along a precipitating gradient. Using the sensitivity obtained from the spatial gradient implies that climate change results in a vegetation shift only between the known biomes within the study region. The assumption may be justified by pollen records or similar studies. In addition, it is important that the ecosystem $\delta^{13}\text{C}$, i.e., $\delta^{13}\text{C}$ averaged from all or dominant species, be

used, rather than $\delta^{13}\text{C}$ of limitedly selected species. This was what we intended to do in the investigation reported here.

A need for correction for the isotopic shift due to organic matter decomposition is for the first time raised by this paper. Although we consider this an important concept, the correction value to be recommended is much less certain. We used the 1.8‰ difference between above-ground vegetation and the surface soil as a basis for calculation in this work, but we stress that this value could either be too high or too low. The value may be too high because it is not corrected for the impact of fossil fuel combustion that has caused the $\delta^{13}\text{C}$ of atmospheric CO_2 to decrease with time since the industrial revolution. It is possible that some fraction of organic matter near the surface is too old to be affected. Due to the bomb ^{14}C input, it is difficult to determine the real age of the surface soil. If we correct for the fossil fuel combustion, the difference between vegetation and surface soil would be 0.5‰ (1.8‰–1.3‰), and the actual value is likely to be between 0.5 and 1.8‰. On the other hand, it is possible that the paleosols investigated have been significantly eroded such that the surface layer is no longer present. The difference between vegetation and deeper soils would be greater than the difference between vegetation and surface soil. In this work, the average difference between vegetation and the deepest soil is estimated to be 2.8‰.

An assumption implied in the correction of decomposition is that paleosols have a pattern of decomposition similar to that observed today. How ^{13}C -enrichment of decomposition is controlled by factors such as climate, types of vegetation, and bacterial community has not been thoroughly studied. One of our earlier investigations (Wang, 2001) included 11 to 12 sites in each of the arid, semiarid and semihumid areas in China. Some of these sites have very poorly developed loess soil. The isotopic difference between vegetation and surface soils is not significantly different among three types of ecosystems, and the mean difference is $2.3 \pm 0.9\%$. This data provide some justification for correcting for the decomposition effect using modern soil profiles, at least on the Loess Plateau of China.

Another question is whether decomposition in C_3 and C_4 vegetation has the same isotopic effect. A two-year litterbag decomposition experiment by Wedin et al. (1995) shows that the $\delta^{13}\text{C}$ of a C_4 grass decreases with time, opposite to the trend of decomposition of C_3 species. However, this was attributed to the fact that the soil underneath of the litterbags had a C_3 isotopic composition. We are not aware of any soil isotopic data derived from pure and stable C_4 ecosystems. This problem remains to be resolved in future studies.

Finally, we should also point out that during correction for the effect of CO_2 concentration on $\delta^{13}\text{C}$ of vegetation bulk organic matter, a direct application of the response of tree-ring $\delta^{13}\text{C}$ to CO_2 concentration may not be reasonable because for tree-ring series the response have been based on $\delta^{13}\text{C}$ analyses of cellulose (Feng and Epstein, 1995). There may be differences in the responses to elevated CO_2

concentration between $\delta^{13}\text{C}$ of cellulose and $\delta^{13}\text{C}$ of vegetation bulk organic matter. As the magnitude of such a potential difference is unknown, we cannot make any correction for it here. This uncertainty may be resolved based on future studies.

5 Conclusions

The ^{13}C -enrichment by decomposition of organic matter can result in overestimation of the percentage of C_4 plants in paleovegetation using $\delta^{13}\text{C}$ values of soil organic matter. This effect has not been considered by previous investigations. This work provides data for quantitative corrections for the decomposition effect by measuring the $\delta^{13}\text{C}$ variation in soil organic matter with depth in 14 soil profiles from three sites. These sites all have C_3 only vegetation, and include both forest and grassland vegetation types. We report that the average $\delta^{13}\text{C}$ difference between soil organic matter and vegetation is 1.8‰ for the surface soil and 2.8 for the bottom soil of our investigated profiles.

The effect of precipitation on $\delta^{13}\text{C}$ of C_3 and C_4 plants has been assessed by a comprehensive investigation of a large number of species (255 of C_3 and 43 C_4 species) from 33 sites in North China, adding additional data to the exiting database for semiarid to semimoiest ecosystems. A strong negative relationship is found between the site-averaged $\delta^{13}\text{C}$ of C_3 plants and the annual rainfall amount with a coefficient of $-0.40\%/100\text{ mm}$, while no significant correlations are observed neither for C_4 plants as a group nor for *Setaria viridis* as a single C_4 species, although $\delta^{13}\text{C}$ shows a slight increase with increasing precipitation.

This study demonstrates that paleovegetation reconstructions can be significantly affected by various corrections to the $\delta^{13}\text{C}_{\text{SOM}}$ value, and to the end member $\delta^{13}\text{C}$ values of C_3 and C_4 plants before using mass balance calculations. We recommend that corrections for changes in $\delta^{13}\text{C}$ of atmospheric CO_2 , ^{13}C -enrichment by decomposition, and changes in precipitation at the given location are made, although sources of error should be evaluated when applied to a given location. Corrections for changes in the atmospheric CO_2 concentration may also be needed, but we currently do not yet have firm knowledge on how much that correction should be. Using these corrections, we show that C_4 plants were likely to be absent during the LG on the central Chinese Loess Plateau, which, considering existing paleotemperature and precipitation data (Wu et al., 1995), is consistent with the distribution of C_4 plants in the modern environment.

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